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USING GEOMETRIC MORPHOMETRICS TO STUDY ONTOGENETIC SHAPE CHANGES IN *PARALEPIDOTUS ORNATUS* (AGASSIZ 1833-43) (ACTINOPTERYGII, SEMIONOTIDAE) (1)

(With 2 figures)

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ABSTRACT: Ontogenetic changes in body shape of the semionotid *Paralepidotus ornatus* were analyzed by the geometric method of partial warps. The coordinates of 13 anatomical landmarks taken on 24 specimens (varying from juveniles to adults) were used to determine the regression of size onto shape, using the method of warp analysis. Most of the ontogenetic allometry occurs along the dorsoventral axis, being represented by an increase of its depth. Ontogenetic transformations along the anteroposterior axis include a compression of the snout, an elongation of the base of the dorsal fin, as well as an elongation of all the posterior-caudal region in adult specimens, with a shortening of the pelvic-anal region.

Key words: Semionotidae, allometry, geometric morphometrics.

RESUMO: Utilizando a Morfometria Geométrica para estudar mudanças ontogenéticas da forma em *Paralepidotus ornatus* (Agassiz 1833-43) (Actinopterygii, Semionotidae).

Mudanças ontogenéticas na forma corporal do semionotídeo *Paralepidotus ornatus* foram analisadas pelo método geométrico de deformações parciais. As coordenadas de 13 marcos anatômicos, tomadas em 24 exemplares (variando de juvenis a adultos), foram utilizadas para determinar a regressão do tamanho sobre a forma usando o método de análise de deformações. Grande parte da alometria ontogenética ocorre ao longo do eixo dorso-ventral do corpo, sendo representada por um aumento de sua altura. Transformações ontogenéticas ao longo do eixo ântero-posterior do corpo incluem uma compressão do focinho, um alongamento da base da nadadeira dorsal, bem como um alongamento de toda a região posterior-caudal nos espécimes adultos, com uma redução da região pélvica-anal.

Palavras-chave: Semionotidae, alometria, morfometria geométrica.

INTRODUCTION

The semionotid *Paralepidotus ornatus* (AGASSIZ, 1833-43) is a marine Norian (Upper Triassic) fish possessing a rather restrict geographical distribution, being so far found mainly in the sedimentary Tethyan deposits of Europe (Italy and Austria). In that region it is well represented, with several complete specimens encompassing different growth stages. Due to the marked difference among juvenile and adult *Paralepidotus,* in the old literature they were often referred to different taxa. Recently, TINTORI (1996, 1998) discussed the ontogenetic variation in this species and pointed out the distinct features. According to him, in *Paralepidotus* the transition from juvenile to adult involves several changes concerning mainly body shape, position of the dorsal fin, dentition, and bone and scale ornamentation. During growth, the body changes from slender and fusiform to deeper and hump-backed, and the dorsal fin origin is more anteriorly positioned.

In this study, ontogenetic changes in *P. ornatus* body shape were analyzed using techniques of geometric morphometrics, that allow a precise comparative analysis of shape and shape changes in organisms using point coordinate data (ROHLF & MARCUS, 1993). Such methods

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represent an interesting alternative to traditional morphometrics, based on measurements of distances and techniques of statistical analysis bivariate and multivariate, being particularly important for studies of systematic, functional morphology and allometry in fishes.

MATERIAL AND METHODS

The analysis was performed on the Cartesian coordinates of 13 two-dimensional landmarks defined on the basis of external morphology of 24 specimens of *P. ornatus*, ranging from 88 to 415mm in standard length (Fig.1). Data were collected from digitized images recorded with a VHSC Panasonic PV-22D camcorder and a Grabit™ frame grabber attached to a notebook computer. The coordinates of the landmarks for each specimen were taken from those images using the TpsDig program, version 1.18, written by F.J.Rohlf.

The geometric size of each specimen was estimated by centroid size, defined as the square root of the sum of squared distances from all landmarks to the centroid of the configuration (BOOKSTEIN, 1991). The landmark coordinates for each specimen were aligned and superimposed by the Procrustes generalized orthogonal least squares method (ROHLF, 1990). In this procedure, the configurations were scaled to unit centroid size and then centered and rotated, in order to minimize the sum of squared distances between the landmarks of each configuration to the corresponding landmarks of a reference or "consensus" configuration, computed as the mean landmark configuration of all specimens.

Patterns of ontogenetic shape changes were analyzed by the thin-plate splines technique (BOOKSTEIN, 1991). This method models shape changes as deformations, by fitting an interpolation function to the aligned landmark coordinates of the specimens against the reference configuration, resulting in a bending energy matrix. The eigenvectors of this matrix are called principal warps, and are relative only to the reference configuration. The eigenvalues associated to each principal warp are inversely related to the spatial scale of shape change, so that large eigenvalues correspond to eigenvectors (principal warps) describing small-scale deformations, whereas small eigenvalues correspond to eigenvectors that describe large-scale deformations. The projection of the Procrustes superimposed specimens onto the principal warps yields the partial-warp scores, that describe their deviations from the reference configuration and can be used as variables in subsequent multivariate statistical analyses (ROHLF, 1996).

The partial-warp scores were regressed onto centroid size, using multivariate regression (MORRISON, 1990). This approach allows to regress several dependent variables (partial warps) onto one independent variable (centroid size), and is more adequate to study allometric

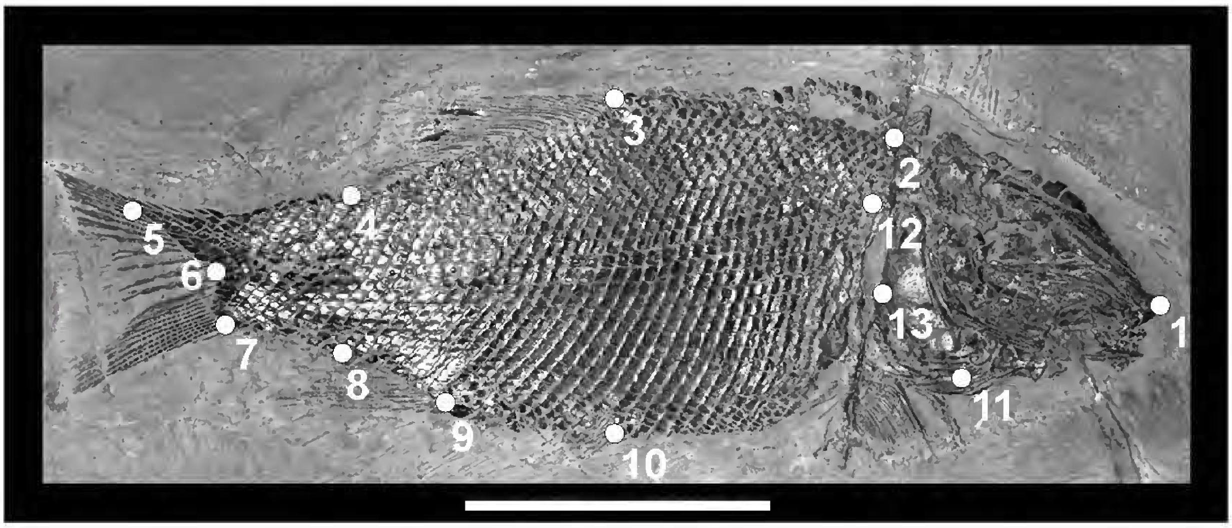

Fig.1- Landmarks collected on *Paralepidotus ornatus* specimens: (1) tip of the snout; (2) anterior edge of the first scale in the dorsal ridge; (3) beginning of the dorsal fin; (4) end of the dorsal fin; (5) posterior edge of the last scale in the superior lobe of the caudal fin; (6) posterior edge of the last scale of the lateral line; (7) ventral edge of the last mid-ventral scale; (8) end of the anal fin; (9) beginning of the anal fin; (10) projection on the ventral margin from point 3; (11) ventral tip of the cleithrum; (12) anterior edge of the first scale of the lateral line; (13) posterior border of opercle. Scale bar = 5cm.

shape changes by geometric methods than the conventional multiple regression with one dependent and several independent variables (ROHLF, 1998). This analysis was done including the uniform components, in order to assess variation in the full shape space (BOOKSTEIN, 1996). The fit of the multivariate regression model was tested using a generalization of GOODALL'S (1991) F-test.

Deformation grids using thin-plate splines were used to graphically portray the patterns of shape variation among the landmarks.

All computations were performed on an IBM-PC compatible microcomputer, with the TpsRegrw program, version 1.19, written by F.J.Rohlf. The morphometric software is available over the Internet from the Stony Brook Morphometrics WWW pages at http://life.bio.sunysb.edu/morph/.

RESULTS AND DISCUSSION

The multivariate regression of partial warps onto centroid size was highly significant (Goodall's F-test = 2.3665, df = 22.484, P < 0.001). Most of the ontogenetic allometry occurs along the dorsoventral axis and it can be interpreted by an uniform increase of the body depth, as depicted by thin-plate splines deformation grids (Fig.2). Ontogenetic transformations also occur along the anteroposterior axis, showing a compression of the snout and an elongation of the base of the dorsal fin, as well as an elongation of all the posterior-caudal region in adult specimens, with a shortening of the pelvic-anal region, thus with the anal fin becoming proportionally more anterior.

These results partially corroborate the intuitive analysis of TINTORI (1996) on the body growth of

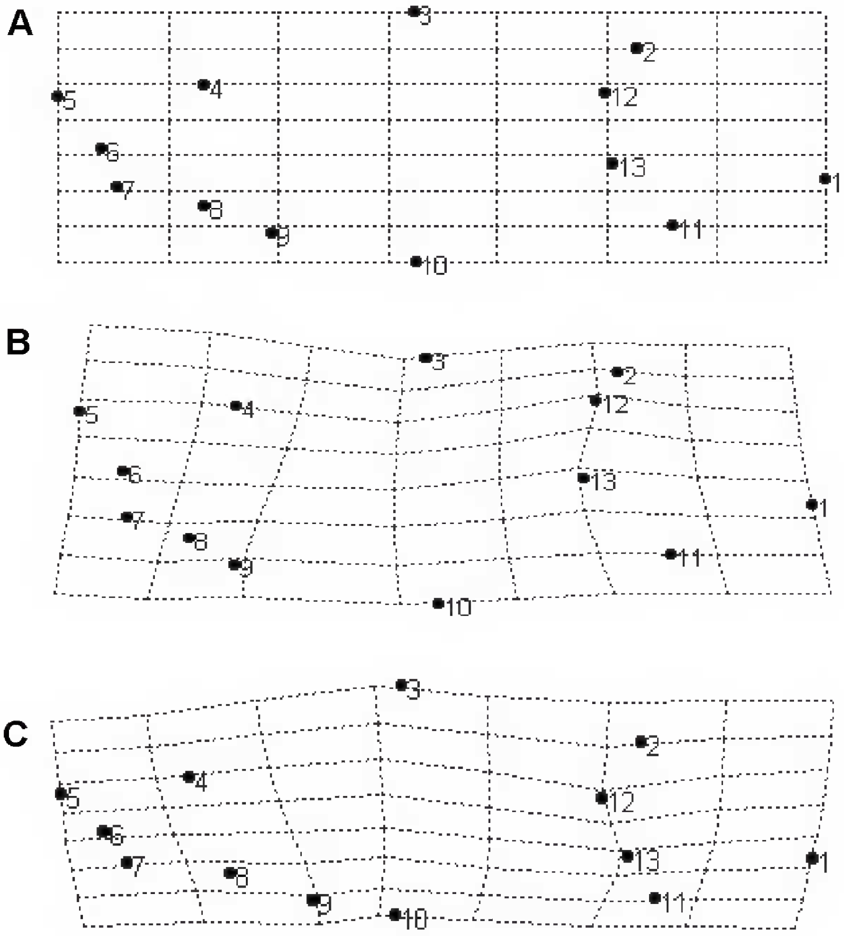

Fig.2- Shape changes, expressed as deformation grids using thin-plate splines, as a function of size in *Paralepidotus ornatus* estimated by a multivariate regression of all shape variables (uniform components+partial warps) on centroid size: (A) consensus configuration; (B) estimated shape for a small specimen (MPUM 7142; SL = 88mm); (C) estimated shape for a large specimen (ST 82911; SL = 415mm).

P. ornatus. However, in our analysis we were able to localize the body regions where the shape changes occur, as well as to indicate the principal directions of variation of form during the ontogeny.

Geometrically the shape changes in *P. ornatus* are not as pronounced as might be suggested by the previous analysis of TINTORI (1996). The allometric growth of the dorsal region originating the typical hump at the beginning of the dorsal fin in most of semionotid fishes could not be detected in the present study with geometric morphometric techniques. Moreover, instead of the relative forward shifting of the dorsal fin origin as suggested by TINTORI (1996), our analysis pointed out an elongation of its base.

The ontogenetic transformations in *P. ornatus* can be related to change in the feeding habit. According to TINTORI (1996, 1998), juveniles were moderately triturant whereas adults were strongly triturant. In this way, the longer insertion of the dorsal fin in *P. ornatus* adults may have been useful for maneuvering near the bottom when feeding on benthic mollusks. Moreover, during the ontogeny the individuals changed the habitat, occupying different positions in the water column. TINTORI (1996) supposed that juveniles lived in more open and superficial waters, whereas adults lived much closer to the bottom along the margins of deep lagoon.

However, it should be emphasized that one of the problems with the relative warps technique, as pointed out by ROHLF (1998), is its dependence of the consensus configuration. In this context, the thin-plate splines deformation grids showed in figure 2 depict indeed the shape differences between the reference configuration and a juvenile specimen (Fig.2B) and an adult specimen (Fig.2C). Therefore, ontogenetic shape changes represented by partial warps should be interpreted with caution, even if using multivariate regression techniques. Notwithstanding, the results of this study emphasize the potential of contemporary geometric morphometric techniques in providing useful insights into the growth patterns of fossil fish.

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